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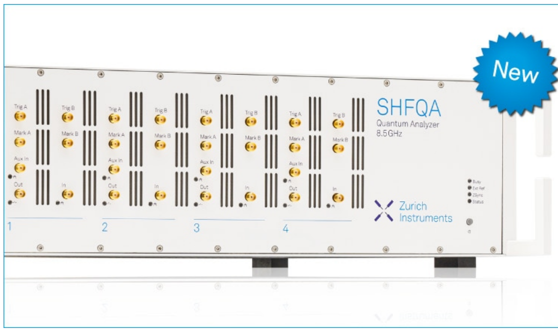

Stochastic Sensitivity Analysis of Noise-Induced Oscillations in Adler Model

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Abstract. We consider Adler model with the saddle-node bifurcation on the invariant circle. Near this bifurcation, even weak random disturbances can generate noise-induced spike oscillations. Corresponding random phase trajectories form stochastic bundle. A dispersion of random trajectories in this bundle is non-uniform. To approximate this dispersion, we propose a new constructive approach based on the stochastic sensitivity analysis and method of "freezing" of the phase variable. A mathematical description of this approach is given. An extension of this theory for complex systems with so-called sequential dynamics is discussed.

INTRODUCTION

The study of the mechanisms of excitability is one of the key problems of modern neuroscience. Nowadays, two basic scenarios of the excitability are specified. The Class I excitability is characterized by the transition from equilibrium to oscillations with the continuously increasing frequency. In the systems with the Class II excitability, oscillations appear with a sufficiently large frequency. From mathematical point of view, these classes of excitability correspond to two types of bifurcations. The Class I excitability is connected with the saddle-node bifurcation on invariant circle (SNIC). Here, the Morris-Lecar neuron model [1, 2] is the well-known example. The Class II excitability is connected with the Andronov-Hopf bifurcation. Here, the classical simple example is the FitzHugh-Nagumo neuron model [3, 4]. In excitable systems, even weak noise can drastically change the behavior [5, 6, 7, 8, 9, 10].

In the studies of the Class I excitability with the SNIC bifurcation, the conceptual model proposed by Adler [11] is widely used. Its modification named a theta-neuron model [12] is a well- studied paradigmatic example of an excitable system in mathematical neuroscience. Various generalizations of such models are extensively explored [13, 14, 15].

In the present paper, we use the stochastic variant of the Adler model to study mechanisms of the excitability and analysis of the probabilistic features of the generated mixed-mode spiking oscillations. In this analysis, the stochastic sensitivity functions technique [16, 17, 18, 19] is used. For the analytical approximation of the dispersion of oscillating random trajectories, we propose a new approach based on method of "freezing" the phase variable. An extension of this theory for complex systems with so-called sequential dynamics [20, 21, 22, 23] is discussed.

TRANSFORMATION OF DETERMINISTIC DYNAMICS

Consider the Adler model defined in polar coordinates by the following system :

$$\begin{aligned} \dot{r} &= a(\varphi) r (1 - r^2), \quad a(\varphi) > 0 \\ \dot{\varphi} &= \varepsilon - \sin\varphi, \qquad \varepsilon > 0. \end{aligned} \tag{1}$$

Here, the function $a(\varphi)$ is 2π-periodic.

The first equation of system (1) has two equilibria $\bar{r}_0 = 0$ and $\bar{r}_1 = 1$. For any function $a(\varphi)$, the equilibrium $\bar{r}_0$ is unstable, whereas the equilibrium $\bar{r}_1$ is stable. As for the whole system (1), the value $\bar{r}_1 = 1$ defines an invariant unit

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circle C (see Fig. 1). For system (1), this manifold is stable. A behavior of system (1) on this manifold is defined by the value of the parameter ε. Here, three cases can be realized.

1) For $0 < \varepsilon < 1$, the second equation has two equilibria $\bar{\varphi}_1 = \pi - \arcsin\varepsilon$ and $\bar{\varphi}_2 = \arcsin\varepsilon$. The equilibrium $\bar{\varphi}_1$ is unstable, and the equilibrium $\bar{\varphi}_2$ is stable. The values $\bar{\varphi}_1, \bar{\varphi}_2$ define for system (1) equilibria $U = (1, \bar{\varphi}_1), S = (1, \bar{\varphi}_2)$. These equilibria lie on the invariant unit circle C (see Fig. 1a): the equilibrium U is unstable (empty circle) and the equilibrium S is stable (black circle).

2) For $\varepsilon = 1$, the equilibria $\bar{\varphi}_1$ and $\bar{\varphi}_2$ of the second equation merge into the single semi-stable equilibrium $\bar{\varphi} = \pi/2$. So, for $\varepsilon = 1$, the system (1) displays on the circle C the single unstable equilibrium $U = (1, \pi/2)$ (see Fig. 1b).

3) For $\varepsilon > 1$, the equilibrium $U = (1, \pi/2)$ disappears and the invariant circle C becomes a limit stable cycle (see Fig. 1c).

Thus, at the point $\varepsilon = 1$, system (1) exhibits the saddle-node homoclinic bifurcation on the invariant circle C. Systems with such type of bifurcation model an important type of the transformation from the equilibrium mode to the spiking one. In system (1), the generated spikes have a constant amplitude, and the interspike intervals decrease as the parameter ε moves away from the bifurcation point $\varepsilon = 1$.

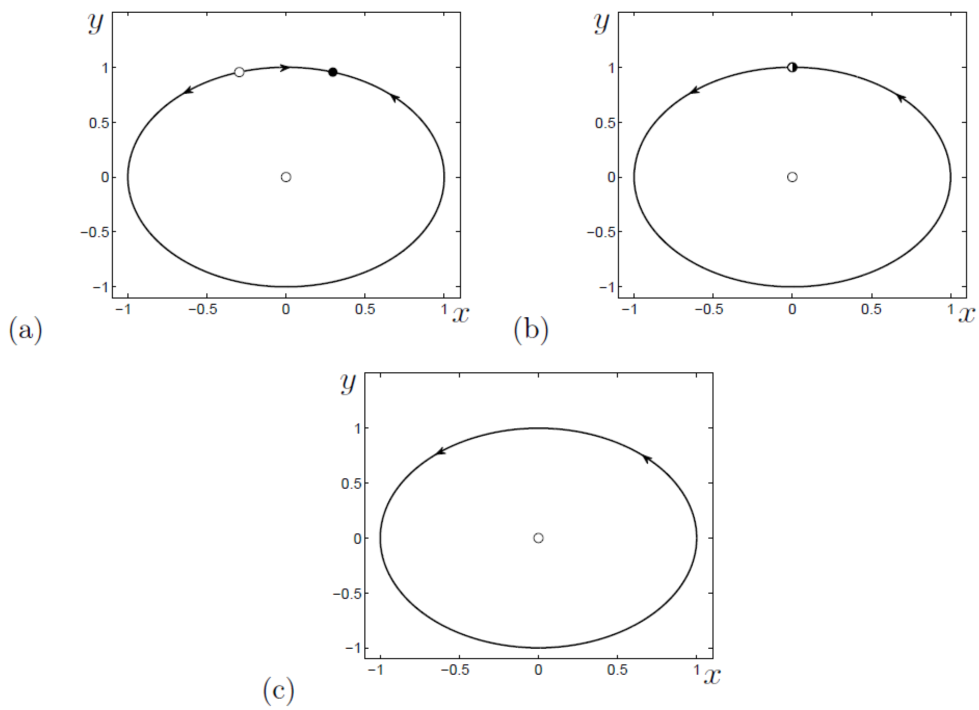

FIGURE 1. Equilibria and invariant unit circle of system (1) for (a) $0 < \varepsilon < 1$, (b) $\varepsilon = 1$, (c) $\varepsilon > 1$. Unstable equilibria are shown by small empty circles, and the stable equilibrium is shown by black circle.

STOCHASTIC EFFECTS

Consider system (1) with additional random disturbances:

$$\begin{aligned} \dot{r} &= a(\varphi)r(1 - r^2) + \sigma_1\xi_1 \\ \dot{\varphi} &= \varepsilon - \sin\varphi + \sigma_2\xi_2. \end{aligned} \tag{2}$$

Here, $\xi_i(t)$ are uncorrelated white Gaussian noises, σ_i are noise intensities. In our study, we use the function $a(\varphi) = 1 + \delta\sin\varphi$ and $\sigma_1 = \sigma_2 = \sigma$.

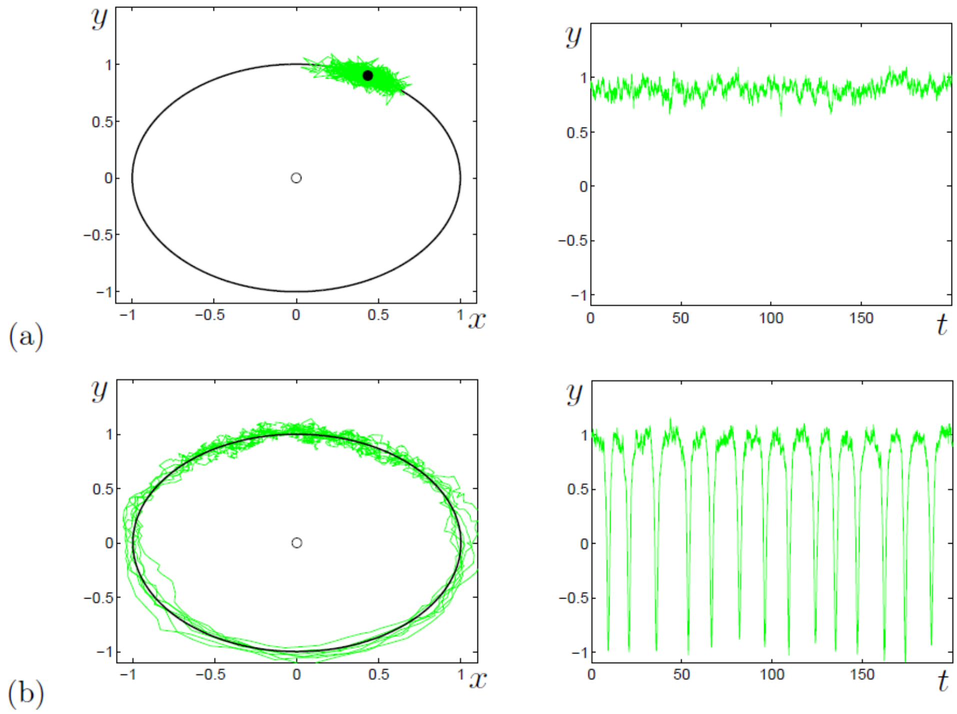

FIGURE 2. Random trajectories and time series (green) of stochastic system (2) with $\sigma = 0.1$, $\delta = 0.1$ for (a) $\varepsilon = 0.9$, (b) $\varepsilon = 1.1$. Here, the stable equilibrium S is shown by black circle.

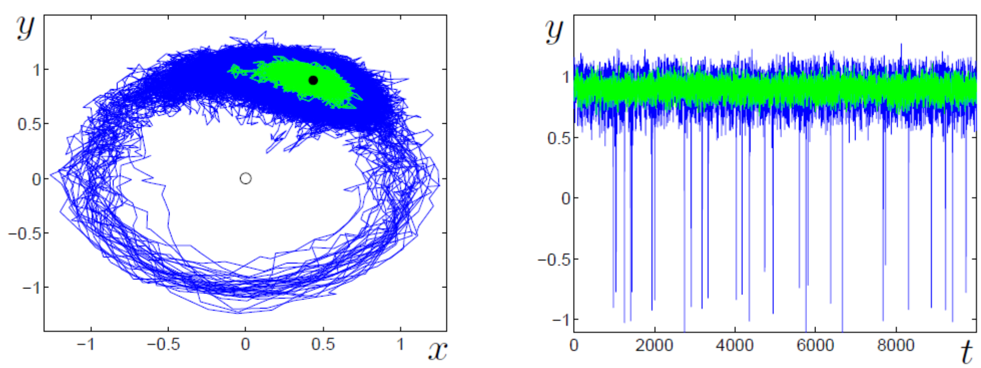

FIGURE 3. Random trajectories and time series of stochastic system (2) with $\varepsilon = 0.9$, $\delta = 0.1$ for $\sigma = 0.1$ (green) and $\sigma = 0.3$ (blue). The stable equilibrium S is shown by black circle.

In Fig. 2, a behavior of system (2) under the week noise is demonstrated for different values of the parameter ε. In the zone $0 < \varepsilon < 1$, the system (1) has the stable equilibrium S as a single attractor. For the small noise intensity, random trajectories of system (2) starting from S concentrate near this point (see Fig. 2a). Corresponding time series exhibit small-amplitude oscillations around this equilibrium.

In the zone $\varepsilon > 1$, the system (1) has the stable limit cycle C as a single attractor. Under the weak noise, system (2) solutions starting from C form a bundle of random trajectories near this attractor (see Fig. 2b). Time series exhibit a mixed-mode regime with the intermittency of small-amplitude oscillations and sharp noisy spikes. Here, the interspike intervals are random.

In the parametric analysis of the dispersion of random states around equilibria and limit cycles, the stochastic sensitivity function technique can be used.

Let $\bar{r}(t) \equiv 1$, $\bar{\varphi}(t)$ be a solution of the deterministic system (1). Let Γ be a phase curve of this solution. The corresponding stochastic sensitivity function $\mu(t)$ in the normal direction to the Γ satisfies the following differential equation:

$$\dot{\mu} = -4(1 + \delta \sin \bar{\varphi}(t))\mu + 1.$$

For the case $0 < \varepsilon < 1$, it holds that $\lim_{t\to\infty} \bar{\varphi}(t) = \bar{\varphi}_2$ and

$$\lim_{t\to\infty} \mu(t) = \frac{1}{4(1 + \delta \sin \bar{\varphi}_2)}.$$

The value

$$\mu = \frac{1}{4(1 + \delta \sin \bar{\varphi}_2)}$$

characterizes the stochastic sensitivity of the stable equilibrium S in the normal direction to the circle C. It can be also shown that the stochastic sensitivity of the stable equilibrium S in the tangent direction to the circle C is defined by the formula

$$m = \frac{1}{2 \cos \bar{\varphi}_2}.$$

In the case $\varepsilon > 1$, the function $\bar{\varphi}(t)$ is 2π-periodic, and the stochastic sensitivity $\mu(t)$ of the limit cycle C at the current point $(1, \bar{\varphi}(t))$ in the normal direction to C satisfies the following boundary problem

$$\dot{\mu} = -4(1 + \delta \sin \bar{\varphi}(t))\mu + 1, \qquad \mu(0) = \mu(2\pi).$$

NOISE-INDUCED EXCITEMENT

Consider the behavior of stochastic system (2) for $\varepsilon < 1$ but close to the bifurcation value $\varepsilon = 1$. In Figure 3, random trajectories of system (2) starting from the equilibrium S are shown for two values of the noise intensity. As one can see, for weak noise $\sigma = 0.1$, random trajectories (green) oscillate near the stable equilibrium S.

For the noise intensity $\sigma = 0.3$, we have qualitatively another type of dynamics. For such a noise, system (2) exhibits mixed-mode regime with the intermittency of small-amplitude oscillations near S and large-amplitude spikes. These spikes appear as a result of large-amplitude loops along the circle C. Such behavior is typical for the phenomenon of the noise-induced excitement. Details of this phenomenon are shown in Figure 4 where x-coordinates of random states of stochastic system (2) are plotted versus σ for three values of the parameter ε. In these figures one can see that when the parameter σ exceeds some threshold value, the large-amplitude oscillations appear. The closer ε to the bifurcation value $\varepsilon = 1$, the lower this threshold.

With the help of the stochastic sensitivity function technique and "three sigma" rule, this threshold σ^* can be estimated analytically:

$$\sigma^* = \frac{\sqrt{2}}{3}(\pi - 2\arcsin \varepsilon)\left(1 - \varepsilon^2\right)^{\frac{1}{4}}.$$

In Figure 5, a plot of the function $\sigma^*(\varepsilon)$ is shown. Here, $\sigma^*(0.9) = 0.28$, $\sigma^*(0.99) = 0.05$, $\sigma^*(0.999) = 0.009$. As one can see, these estimations well agree with results of direct numerical simulations shown in Figure 4.

STOCHASTIC SENSITIVITY OF NOISE-INDUCED SPIKING OSCILLATIONS

For $\varepsilon < 1$ but close to the bifurcation value $\varepsilon = 1$, equilibria $\bar{\varphi}_1$ and $\bar{\varphi}_2$ of the second equation of system (1) are close to each other. In the interval $(\varphi_1, \varphi_2) = (\bar{\varphi}_1 + r, \bar{\varphi}_2 - r)$, the function in the right side of the equation $\dot{\varphi} = \varepsilon - \sin \varphi$ is rather small. So, in this interval, the randomly forced variable $\varphi(t)$ changes slowly, much slower than the trajectory tends to the circle C along the normal.

Applying the method of "freezing" of the variable φ in the interval (φ_1, φ_2), one can find the stochastic sensitivity of the circle C by the formula

$$\mu(\varphi) = \frac{1}{4(1 + \delta \sin \varphi)}.$$

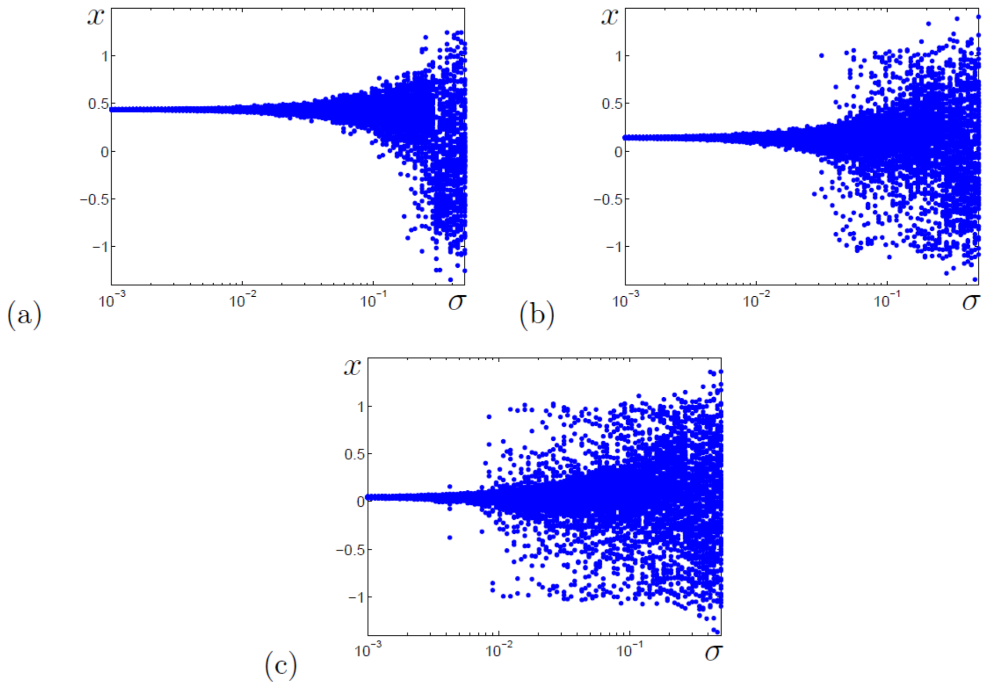

FIGURE 4. Random states of stochastic system (2) with $\delta = 0.1$ for (a) $\varepsilon = 0.9$, (b) $\varepsilon = 0.99$, and (c) $\varepsilon = 0.999$.

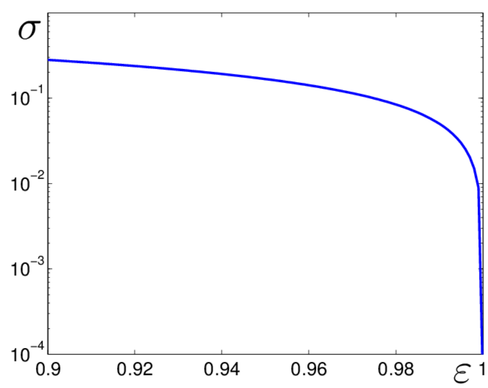

FIGURE 5. Plot of the threshold function $\sigma^*(\varepsilon)$ for system (2) with $\delta = 0.1$.

In order to find the stochastic sensitivity at the other points of C, we have to solve the following differential equation

$$\dot{\mu} = -4(1 + \delta \sin \bar{\varphi}(t))\mu + 1,$$

where

$$\bar{\varphi}(0) = \varphi_1, \quad \mu(0) = \frac{1}{4(1 + \delta \sin \varphi_1)}.$$

To avoid the calculation of $\bar{\varphi}(t)$, one can use the variable φ instead of t:

$$\frac{d\mu}{d\varphi} = \frac{-4(1 + \delta \sin \bar{\varphi})\mu + 1}{\varepsilon - \sin \varphi}, \qquad \mu(\varphi_1) = \frac{1}{4(1 + \delta \sin \varphi_1)}.$$

An efficiency of this method are illustrated in Figure 6. Here, the theoretical stochastic sensitivity function $\mu(\varphi)$ is plotted by solid lines, and the results of the direct numerical calculation are shown by asterisks.

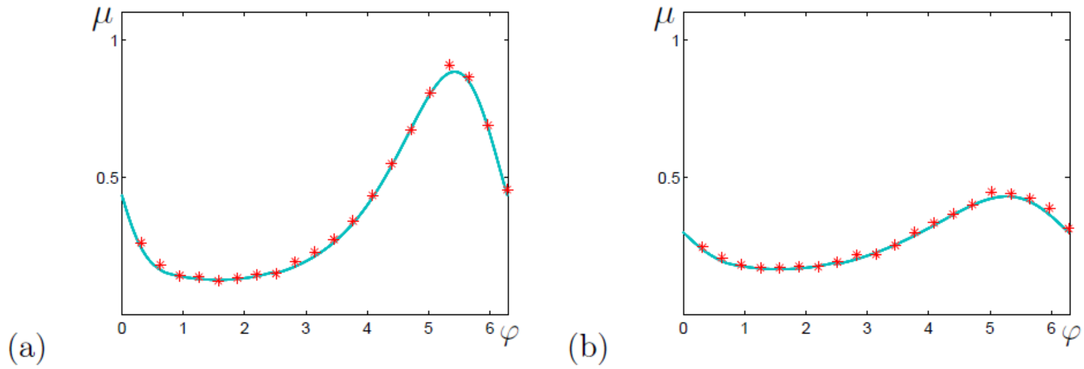

FIGURE 6. Stochastic sensitivity of noise-induced spiking oscillations of stochastic system (2) with $\varepsilon = 0.99$, $\sigma = 0.05$: (a) for $\delta = 0.95$, (b) $\delta = 0.5$.

As can be seen, the suggested method of the stochastic sensitivity analysis of noise-induced spiking oscillations in the zone where the deterministic system possesses the stable equilibrium only, well agrees with results of the numerical simulation of random trajectories.

Conclusion

In the analysis of the underlying mechanisms of stochastic phenomena in nonlinear systems, an important role is played by the simple conceptual dynamical models. One of such models is the Adler model which mimics the Class I excitability of neuron dynamics. On the base of this model, we studied the mechanism of the stochastic excitement near the saddle-node bifurcation on the invariant circle. We show how the stochastic sensitivity technique can be constructively used in the investigation of the noise-induced phenomena. Here, in the analysis of noise-induced spiking oscillations, the method of "freezing" of the phase variable was effectively used. This approach is readily applicable for the study of stochastic phenomena in complex systems with so-called sequential dynamics.

Acknowledgments

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